



Nest structure, pollen utilization and parasites associated with two west-Mediterranean bees (Hymenoptera, Apiformes, Megachilidae) nesting in empty snail shells

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Abstract

Around thirty species of European solitary bee species in the family Megachilidae nest in empty gastropod shells. We surveyed this group of bees in semi-natural sites adjacent to almond orchards near Lleida (north-eastern Spain) and collected 35 *Hoplitis fertoni* and 58 *Osmia ferruginea* nests in shells of six snail species. We describe the nest structure and report the identity of pollens collected by the two bee species. Both species adjust the number of brood cells to the size of the shell and occasionally build intercalary (empty) cells. *H. fertoni* uses clay and *O. ferruginea* chewed plant leaves for building cell partitions and nest plugs. Most nests of both species were built in *Sphincterochila candidissima* shells. Analysis of the pollen of selected nests confirmed that *H. fertoni* is oligoleptic on Boraginaceae (in our study all pollen was from *Lithodora fruticosa*) and *O. ferruginea* is a polyleptic species (collecting mostly pollen from Cistaceae, Fabaceae, and Lamiaceae in our study area). Nests of *H. fertoni* were parasitized by five species, the golden wasp *Chrysura hybrida*, the cuckoo bee *Dioxys moesta*, the velvet ants *Stenomutilla collaris* and *Stenomutilla hotentotta*, and the bee-fly *Anthrax aethiops*; nests of *O. ferruginea* were parasitized by the sapygid wasp *Sapyga quinquepunctata* and *A. aethiops*. Except for *C. hybrida* these are newly recorded host-parasite associations. Our results confirm previous information and bring new findings on the ecology of both species.

Keywords

Spain, Lleida, *Hoplitis fertoni*, *Osmia ferruginea*, parasitoid, cleptoparasite, pollen specialization

Introduction

Bees (Anthophila/Apiformes) are a very speciose clade of Hymenoptera, with more than 20,000 species worldwide (Michener 2007). Most of these species are solitary and build their nests underground (Michener 2007; Danforth et al. 2019). However, about a third of the solitary bee species nest above-ground, mostly in pre-established cavities (Bogusch and Horák 2018). Among these, a small group of species have specialized in nesting in empty gastropod shells. This behaviour is widespread in the Old World (Müller et al. 2018), including the Palaearctic and Southern Africa (Gess and Gess 1999, 2008), but much rarer in the New World (Michener, 2007). In Europe about 30 species in the genera *Osmia*, *Hoplitis*, *Protosmia* and *Rhodantidium* are known to construct nest in gastropod shells. The majority of these species have distributions restricted to the southernmost part of the continent (Müller 1994; Müller et al. 2018). Most of these species are very specialized in their nesting substrate choice and rarely use other cavity types (but see Bosch et al. 1993). The nesting biology of species occurring in central Europe is fairly well-known. Several species display a series of behaviours related to the manipulation, translocation, and camouflaging of the nest shells (Bellmann 1981; Müller et al. 2018). Various species of *Chrysura* golden wasps have been reported as parasitoids of these species (Müller 1994; Westrich 2018; Bogusch et al. 2019). However, the nesting biologies of species occurring only in southern Europe remain poorly known (Müller et al. 2018). During our studies on shell-nesting bees near Lleida (Catalonia) in northeast Spain we collected a good number of nests of *Hoplitis fertoni* and *Osmia ferruginea*, two species with a Mediterranean distribution.

Hoplitis fertoni occurs in North Africa, Spain, Portugal, and Sicily, and may be locally abundant. It builds its nests in shells of large snail species (such as *Eobania*, *Otala* and *Theba*), and uses mud to build brood cell partitions and to close the nest (Ferton 1908; Le Goff 2003; Müller et al. 2018). *H. fertoni* nests in spring and does not move or cover its nesting shells (Le Goff 2003). Cuckoo wasps *Chrysura hybrida*, *Chrysura cuprea* and *Chrysura trimaculata* are parasitoids of *Hoplitis fertoni* and several other bees nesting in empty shells (Berland and Bernard 1938; Petit 1969, 1980; Le Goff 2003; Wiśniowski 2014).

Osmia ferruginea occurs in all countries around the Mediterranean and may be locally common in the West-Mediterranean region (Müller 2019). It flies in the spring and utilizes shells of a high number of snail species of various sizes, where it builds 1–10 brood cells separated by partitions of masticated plant matter (Ferton 1905; Saunders 1908; Alfken 1914; Benoist 1931; Mavromoustakis 1952; Grandi 1961; Haesseler 1997; Moreno-Rueda et al. 2008). Although this species is widespread in South Europe, no associated parasitoid species are known (Müller 2019).

Here, we describe the nest structure of *Hoplitis fertonii* and *Osmia ferruginea*, and report on the snail shells used and the pollens collected by these two species. We also report on several parasitoids and nest cleptoparasites reared from the collected nests. We discuss our results in relation to previous information available for these two species (Ferton 1905, 1908; Benoist 1931; Grandi 1961; Haesseler 1997; Le Goff 2003; Moreno-Rueda et al. 2008; Müller et al. 2018; Müller 2019).

Methods

In March 2019 we collected more than 500 large gastropod shells (the size of semiadult *Cernuella virgata*, 8 mm, or bigger) in 10 semi-natural sites with high shell availability around almond orchards near Lleida. We also collected 434 shells in three additional localities in which shell availability was lower. Some of the shells contained *Hoplitis fertonii* nests built in the previous year (with cocoons). Other shells contained fresh *Osmia ferruginea* nests (with provisions and eggs/larvae).

Hoplitis fertonii nests were dissected 0–8 days after collection. The number of brood cells, their shape and positions within the shell and the number of larvae, pupae and adults were recorded. Some remnants of pollen provisions were collected and placed inside plastic micro-tubes for later identification. Some *O. ferruginea* nests were also dissected 0–8 days after collection. The rest were dissected at biweekly intervals until May 11th, when all nests contained mature larvae in cocoons (prepupae). All brood was kept under laboratory conditions until adult eclosion which occurred by September the same year. The cocoons were opened in September 2019, when all bees and their parasites developed into adults and were alive inside the cocoons, two specimens of the brood parasite *Sapyga quinquepunctata* spontaneously hatched and left the cocoons a few days before we opened them.

Pollen samples were prepared using a standard acetolysis method (Moore et al. 1991). Pollen were boiled for 5 min. in an acetolysis mixture of sulphuric acid (H_2SO_4) and acetic anhydride (CH_3CO_2O) (1 : 9 ratio). Samples were then transferred to a mixture of water and glycerol. Slides were observed at 400 \times magnification. Pollen grains were determined using pollen identification keys (Punt and Clarke 1984; Moore et al. 1991; Reille 1992; Beug 2004) and the reference collection of the Institute of Botany of the Czech Academy of Sciences.

Photos of shells containing nests, closing plugs, and dissected nests were taken with a digital camera Nikon Coolpix B500. Photos of larvae, brood cells, and nest details were taken with a digital camera Canon EOS 550 and a macro-objective equipped with LED goose-neck light. Final figures were created from multiple level-photos stacked by Zerene Stacker software. We drew figures of nest structure using pen-drawing and colouring in Adobe Photoshop. Photos of pollen grains were taken under a light microscope Delphi X-Observer DX 2153-PLi with a camera Moticam 5+ and software for photo analysis.

Results

Hoplitis fertoni

Nest structure. We collected 35 gastropod shells with nests of *H. fertoni* in three of the 13 localities surveyed. All of the localities were situated in dry hilly region. All shells were found on the ground surface and were not hidden. The closing plug was made of soil of light-brownish or greyish colour (Fig. 1A). In most nests (32) the closing plug was placed at the shell aperture. In the remaining three shells it was placed a few mm inside the shell. Several nests had a vestibular (empty) cell below the plug. The rest of the shell was filled with brood cells. Some nests had one or more empty intercalary cells. The brood cell walls were fully lined with soil and inter-cell partitions were double (Fig. 1D). The brood cells were arranged longitudinally along the spire of the shell cavity but some nests had two or more cells arranged transversally close to the nest aperture. Brood cell partitions were 2–5 mm thick (mean 2.6 mm) and the closing plug 3.5–8 mm thick (mean 4.9 mm) (Fig. 1D).

Shell choice. The majority (26, 74.3%) of the nests were built in shells of *Sphincterochila candidissima*. Other snail species used were *Eobania vermiculata* (4, 11.4%), *Cernuella* sp. (3, 8.6%) and *Otala lactea* (1, 2.9%). The 35 nests collected contained 217 brood cells (mean \pm SD: 6.2 ± 2.24 ; range: 2–10 brood cells per nest). The nests in *S. candidissima* shells contained 4–9 brood cells (mean 6.4, median 7), and those in *E. vermiculata* shells 5–10 brood cells (mean 5.8, median 6). Nests in the smaller *Cernuella* sp. shells contained fewer cells (range 2–3, mean 2.3, median 2).

Nest associates. Altogether 58 (26.7%) brood cells contained dead, dry or mouldy contents. Of the remaining brood cells, 126 contained pupae or adults of *H. fertoni*, and 33 were parasitized (25.8% of brood cells containing live insects). The golden wasp *Chrysura hybrida* (Chrysidae) was the most common parasitoid (21 cells in 14 nests). Cells parasitized by *C. hybrida* were recognizable by the presence of a semi-transparent brownish cocoon with a whitish spot within the thicker brownish cocoon of *H. fertoni*. We also found five nests parasitized by the velvet ant *Stenomutilla collaris* (seven cells) and one nest by *Stenomutilla hotentotta* (one cell) (Mutillidae). Velvet ants pupated and became adults by late spring (late May – June). *Stenomutilla* cocoons were very similar to those of *C. hybrida* but harder and darker and did not have whitish marks. We also found three nests parasitized by the cuckoo bee *Dioxys moesta* (Megachilidae) (one cell per nest). The cocoons of this species were composed of a single whitish layer sparsely covered with dark brownish faecal particles. Pupation and adult eclosion occurred more or less at the same time as in *H. fertoni*. Finally, we found one nest with one cell parasitized by the bee-fly *Anthrax aethiops* (Bombyliidae). The structure of all nests is illustrated in Fig. 2.

Pollen contents. We analysed pollen samples (remnants of unconsumed provisions) from six nests from two localities (S35 and S37). All pollen grains identified were *Lithodora fruticosa* (Boraginaceae) (Fig. 3A). During of March 2019 we repeatedly observed *Hoplitis fertoni* females collecting pollen only on flowers of this species in various localities.

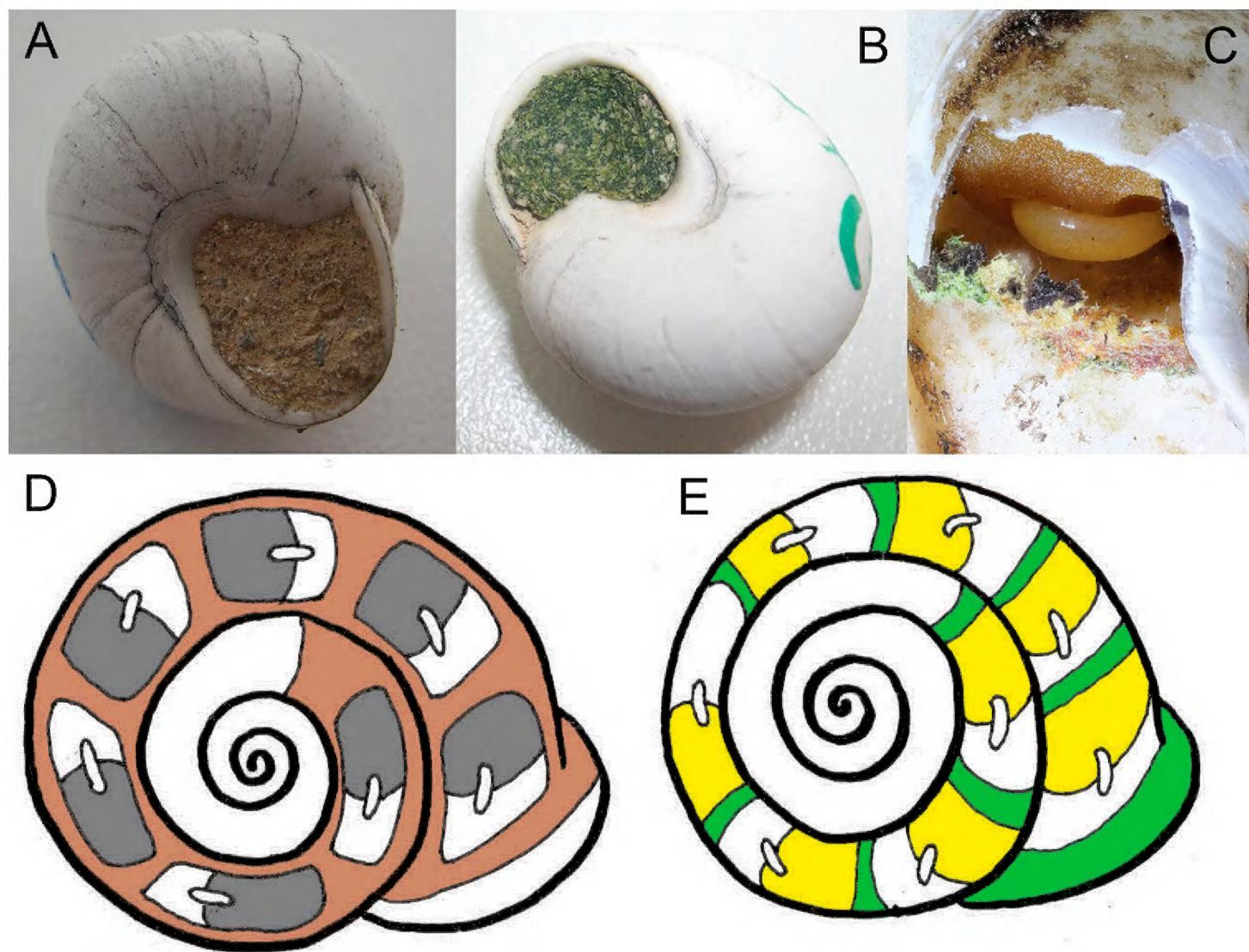


Figure 1. Structure of *Hoplitis fertoni* (A, D) and *Osmia ferruginea* (B, C, E) nests **A** shell of *Sphincterochila candidissima* with nest of *H. fertoni* **B** shell of *S. candidissima* with nest of *O. ferruginea* **C** larva of *O. ferruginea* on pollen-nectar provision **D** nest structure of *H. fertoni* **E** nest structure of *O. ferruginea*. Photos and drawings by P. Bogusch.

Osmia ferruginea

Nest structure. We collected 58 shells with nests of *O. ferruginea* in nine of the 13 localities surveyed. Most nests (48) were collected in the localities of a dry hilly area. The remaining 10 nests were collected in the river floodplains. All nests were found exposed (not hidden) at ground level. The surface of the shells had no traces of masticated leaf matter. The closing plug was made of green masticated leaf matter (Fig. 1B). In most nests (38) it was placed at the shell aperture, but in some it was placed inside the shell. All nests had a vestibular (empty) cell below the plug. Brood cells were separated by narrow single partitions of masticated plant matter and the side walls of the brood cells were not lined (Fig. 1C). At the time nests were dissected (March 2019), each cell contained a yellow to light yellow spherical pollen provision with an egg or a young larva (Fig. 1C). The brood cells were always placed longitudinally along the spire of the shell. Brood cell partitions were around 1 mm thick and the closing plug 1.5–3 mm thick (mean 2.1 mm) (Fig. 1E).

Shell choice. Most nests (28, 48.3%) were built in *Sphincterochila candidissima* shells. The remaining nests were placed in shells of *Eobania vermiculata* (13, 22.4%),

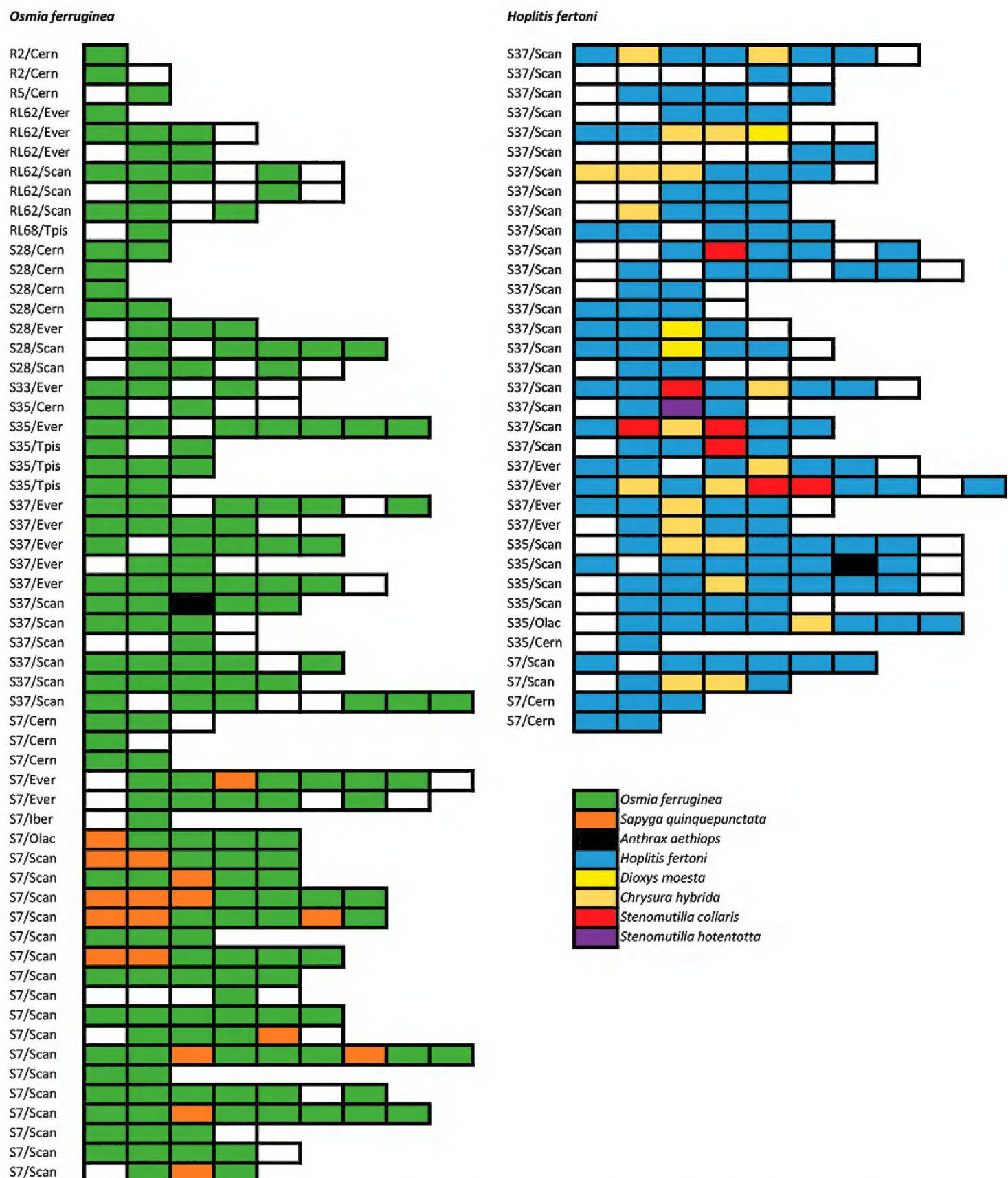


Figure 2. Diagrams of nest structures of nests of *Hoplitis fertonii* (right) and *Osmia ferruginea* (left). The nests are identified by locality snail codes (Cern – *Cernuella* sp., Ever – *Eobania vermiculata*, Iber – *Iberellus* sp., Olac – *Otala lactea*, Scan – *Sphincterochila candidissima*, Tpis – *Theba pisana*). Each box represents one brood cell, starting with the innermost cell on the left. Colours represent the various species recorded. White boxes represent intercalary cells.

Cernuella sp. (11, 18.9%), *Theba pisana* (4, 6.9%), *Iberellus* sp. (1, 1.7%) and *Otala lactea* (1, 1.7%). The 58 nests collected contained 268 brood cells (mean \pm SD: 4.6 \pm 2.09; range: 1–9 brood cells per nest). The nests in *S. candidissima* shells contained 2–9 brood cells (mean 5.6, median 5), and those in *E. vermiculata* shells were similar 1–9 brood cells (mean 5.5, median 6). Nests in the smaller shells of *Cernuella* sp. and

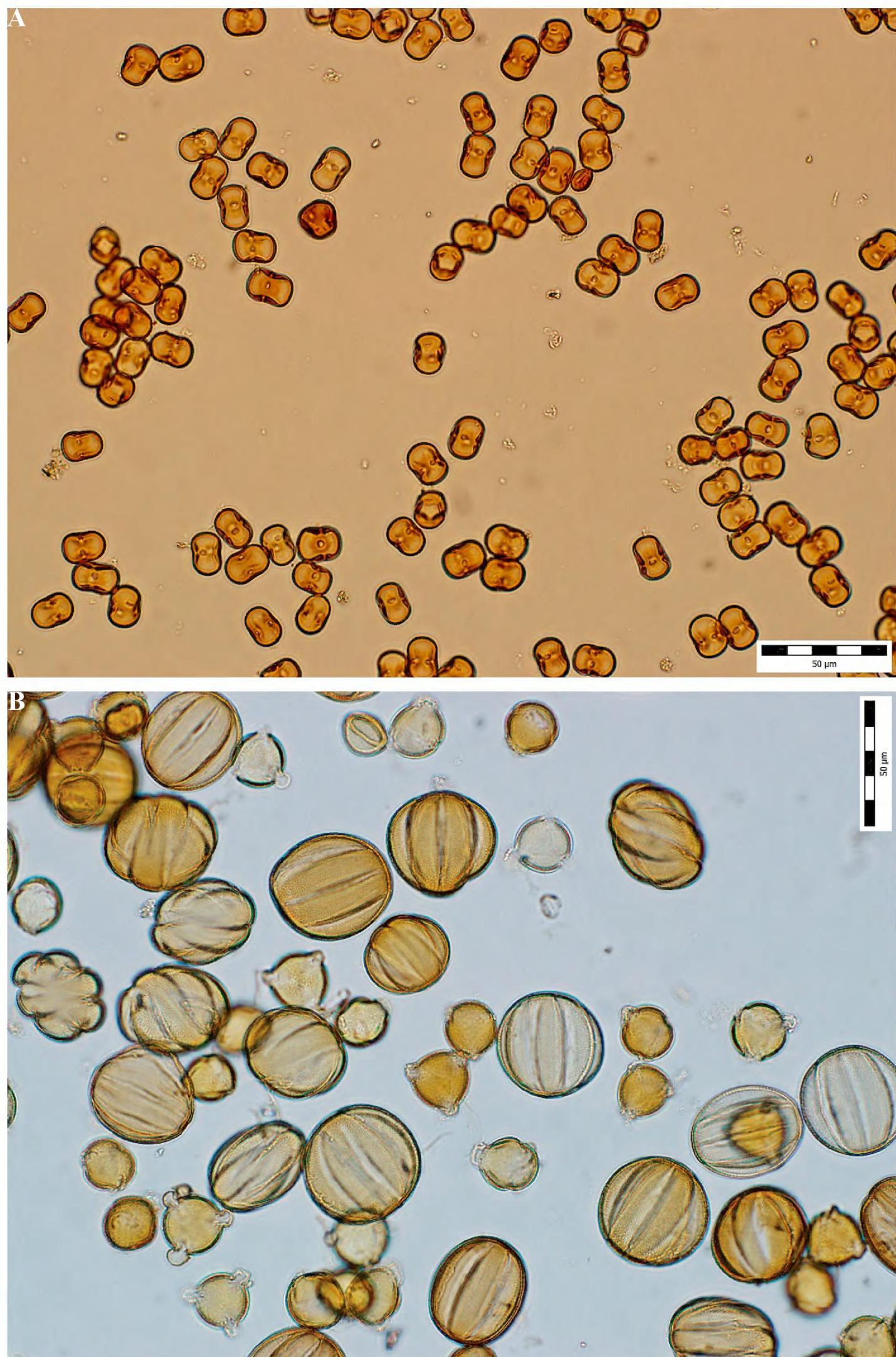


Figure 3. A Macrophotography of pollen of *Lithodora fruticosa* from a *Hoplitis fertoni* nest (locality S35). Photo by L. Petr. **B** macrophotography of pollen from an *Osmia ferruginea* nest (locality S7). Larger pollen grains are *Thymus vulgaris*; smaller grains are *Cistus albidus*. Photo by L. Petr.

Table 1. Pollen composition of six provision samples from *Osmia ferruginea* nests.

Site	Pollen contents
S35	<i>Cistus albidus</i> (Cistaceae) ca. 100%, Asteraceae and <i>Thymus vulgaris</i> (Lamiaceae)
S37	<i>Cistus albidus</i> (Cistaceae) 37 %, <i>Cytisus scoparius</i> (Fabaceae) 37 %, <i>Olea europaea</i> (Oleaceae) 26 %
S37	<i>Cistus albidus</i> (Cistaceae) 50%, <i>Cytisus scoparius</i> (Fabaceae) 40%, <i>Olea europaea</i> (Oleaceae) 10%
S7	<i>Cistus albidus</i> (Cistaceae) 48 %, <i>Cytisus scoparius</i> (Fabaceae) 27 %, <i>Olea europaea</i> (Oleaceae) 22 %, <i>Thymus vulgaris</i> (Lamiaceae) 12 %, contamination of three pollen types of Asteraceae
S7	<i>Thymus vulgaris</i> (Lamiaceae) 51 %, <i>Cytisus scoparius</i> (Fabaceae) 49 %
S7	<i>Cytisus scoparius</i> (Fabaceae) 77 %, <i>Thymus vulgaris</i> (Lamiaceae) 23 %

T. pisana contained fewer cells (range 1–5, mean 2.1, median 2 and range 2–3, mean 2.5, median 2–3, respectively).

Nest associates. Altogether 56 (20.9%) of the brood cells contained dead, dry or mouldy contents. Most of the remaining brood cells (203) contained pupae or adults of *O. ferruginea*, while 19 contained parasitoids (9% of brood cells containing alive insects). The main parasitoid species was *Sapyga quinquepunctata* (Sapygidae; 18 cells from 11 nests, all from locality S7; 19% parasitism). All the individuals of this cleptoparasitic species reached adulthood by late summer or beginning of autumn (September). Brood cells parasitized by *S. quinquepunctata* were recognizable by the dark brown oval-shaped cocoon, distinct from the cubic cocoons of *O. ferruginea*. The bombyliid *Anthrax aethiops* was recorded in a single cell of one nest. The structure of all nests is illustrated on Fig. 2.

Pollen contents. We analysed six pollen samples from nests collected at three different localities. Most pollen grains were of Cistaceae, Fabaceae (*Cytisus* type), and Lamiaceae (Table 1; Fig. 3B).

Discussion

Nest structures of both species correspond to the nest descriptions published by previous authors (Ferton 1905, 1908; Benoist 1931; Grandi 1961; Haesseler 1997; Le Goff 2003; Moreno-Rueda et al. 2008; Müller et al. 2018; Müller 2019). Both *Hoplitis fertonii* and *Osmia ferruginea* belong to the group of species building high numbers of brood cells per nest. Most bee species nesting in empty gastropod shells build low numbers of brood cells per shell (usually only one or two) (see Müller et al. 2018). The number of brood cells per nest in both *Hoplitis fertonii* and *Osmia ferruginea* is highly variable depending on the size of the shell utilized. Compared to other middle-sized bee species such as *Osmia rufohirta*, which usually nests in shells of *Xerolenta obvia* and builds one brood cell per nest (Bellmann 1981; Müller et al. 2018; Heneberg et al. 2020), *Hoplitis fertonii* and *Osmia ferruginea* seem to prefer bigger shells (specially *Sphincterochila candidissima*) and build a higher number of cells per nest. *S. candidissima* has also been reported as the most commonly used shell in other studies on shell-nesting bees (Moreno-Rueda et al. (2008), Bogusch et al. (in press)).

The number of parasitic species associated with *H. fertoni* (5) in our study is remarkable. The most common parasitoid, *Chrysura hybrida* was already recorded on *H. fertoni* by Le Goff (2003). This species has been associated to several other Osmiini, nesting either in snail shells (*Osmia versicolor*, *Osmia viridana*) or in other types of cavities (*Hoplitis anthocopoides*, *Hoplitis benoisti*, *Hoplitis ravouxi*, *Osmia caerulescens*, and *Anthocopa villosa*) (Berland and Bernard 1938; Grandi 1961; Petit 1969, 1980). Most of these records are based on observations of the bee and the wasp co-occurring at a given locality but, together with our findings, they suggest that *C. hybrida* specializes on smaller Osmiini, irrespective of the nesting substrate. Other species of *Chrysura* also parasitize bees of the family Megachilidae, and many of them appear to show a strong preference for bees nesting in snail shells (see Müller et al. 2018).

We also reared two species of velvet ants from the nests of *H. fertoni*. Velvet ants are ectoparasitoids and usually have a broad host spectrum. Some species preferentially parasitize either bees or wasps, but others have been recorded on both guilds of hymenopterans (Lelej 1985; Brothers 1989; O'Neill 2001). The biology of *Stenomutilla* is not well-known, but several authors have reported associations with solitary wasps, megachilid bees and chrysomelid beetles of the subfamily Clytrinae (Giner Marí 1944; Brothers 1989). Thus, it is likely that both species of *Stenomutilla* recorded in our study parasitize a wide range of bees and possibly wasps. However, in a broader study in the same geographical area we have examined hundreds of nests of more than ten snail-nesting bees and we found *Stenomutilla* only in nests of *H. fertoni* (Bogusch et al., in press).

The bee-fly *Anthrax aethiops*, has been recorded as a parasitoid in nests of more than ten bee species, some of them nesting in gastropod shells (Austen 1937; Du Merle 1972; Peeters et al. 2012; Müller et al. 2018). Heneberg et al. (2020) found this species to be a frequent parasitoid of *Osmia spinulosa* and two other species nesting in gastropod shells. This parasitoid has probably a broad host spectrum mostly including megachilid bees but also other bees. Although this species has only been reported as a parasitoid of bees, many other representatives of this family are beside bees parasitoids of crabronid wasps (Yeates and Greathead 1997; Bogusch et al. 2015).

Dioxys moesta is a cuckoo bee occurring in south Europe and North Africa. Its host spectrum is unknown. Other *Dioxys* species in Europe and neighbouring regions, are cleptoparasitic on bees of the family Megachilidae, mostly *Hoplitis* and *Osmia* (Westrich 2018), but up to now they were not known to parasitize species nesting in shells. The question whether *D. moesta* specializes on shell-nesting species remains open.

Sapyga quinquepunctata is an unspecialized cleptoparasite in nests of several Megachilidae (Stöckhert 1933; Vicens et al. 1993; Vicens et al. 1994; Gusenleitner and Gusenleitner 1994; Osorio et al. 2018; Müller et al. 2018; Torné-Noguera et al. 2020). Although it has been reared from nests of *Osmia bicolor* (Westrich 2018; Heneberg et al. 2020), it does not appear to be common in nests of shell-nesting species (Bogusch et al. 2019; Heneberg et al. 2020). Our findings of *S. quinquepunctata* and *Anthrax aethiops* in nests of *O. ferruginea* represent the first records of nest parasitism in this species.

Analysis of the pollen provisions yielded contrasting results for the two species studied. Previous studies have reported *Echium* (Boraginaceae) as the only pollen

source of *H. fertoni* (Le Goff 2003, Sedivy et al. 2013; Müller 2019). Both pollen analysis and field observations indicate that in the study area this species visits another Boraginaceae, *Lithodora fruticosa*. Thus, with the information currently available, *H. fertoni* should be considered oligoleptic on Boraginaceae, just like most species of the *Hoplitis adunca* species-group (Müller 2019). We have also observed flowering *L. fruticosa* at five localities studied, and three females of *H. fertoni* in three localities (one in each) were observed on flowers of this plant. No species of *Echium* was in flower during our studies (middle March 2019) so *L. fruticosa* is probably the only useful source of pollen for first females of *H. fertoni* provisioning their nests. In other regions, the situation can be different and this species can specialize on other pollen sources, especially of genus *Echium* (as was published by Le Goff 2003 and Müller et al. 2018). *H. fertoni* lacks any of the morphological adaptations usually present in bees that harvest pollen from flowers with included anthers, so it is a question how it is able to efficiently exploit these flowers. Perhaps some behavioral trick that might be revealed by detailed field observation. On the other hand, our results confirm that *O. ferruginea* is a polyleptic species with preference for the Fabaceae (Müller 2019). In our nests, all provisions analyzed contained pollen from several plant families. Other species in the subgenus *Pyrosmia* are usually polyleptic, but several are oligoleptic on Fabaceae (Müller 2019).

The biology of shell-nesting bees from south Europe is poorly known. Our study contributes to filling this gap by providing new records of parasites and pollen use, as well life history and nesting behaviour traits. Interestingly, some of these traits are shared with bees of the same taxa nesting in other types of cavities. For example, *Hoplitis adunca* also lines cell walls, builds double inter-cell partitions and is oligoleptic on Boraginaceae (Bosch et al. 2001). For the most part, parasites recorded in this study also seem to be shared by species nesting in other substrates. Nesting behaviour, pollen preferences and host-parasite associations are important sources of information for the reconstruction of phylogenies and for tracking the evolution of behavioural traits in Megachilid bees (Müller 1996; Bosch et al. 2001; Sédivy et al. 2008, Litman et al. 2011; González et al. 2019).

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